SECONDARY PRODUCTIVITY OF TERRESTRIAL ECOSYSTEMS
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3.3.1 Community metabolism of soil invertebrates in forest ecosystems of Japan

1. INTRODUCTORY REMARKS

An important rôle of soil fauna in the terrestrial ecosystem is in the decomposition of litter, and the greater the activity of soil fauna the greater is the productivity or rate of production of the ecosystem. This is in sharp contrast to the destructive nature of the grazing activity of the animals above the ground surface. In this study, I have chosen primeval or natural forest as the working field, because the natural "climax" vegetation is the control area against the man-made field and grassland, secondary or artificial forest of the region.

Three forest ecosystem types appear along a thermal or altitudinal gradient in Central Japan where there is high rainfall (Tab. I). Preliminary investigations were carried out for some years on the bio-economics of the soil animal community in these ecosystem types. The principal aim of this paper is to point out from these preliminary studies some important methodological problems concerning the relation of community metabolism of soil animals to the whole ecosystem metabolism. The determination of ecosystem types, estimation of primary productivity and litter supply, decomposition of litter and humus by soil animals as well as assimilation, respiration and mortality are taken into special consideration here.

2. WORK IN THE SUBALPINE CONIFEROUS FOREST ECOSYSTEM

A working field was selected on a plateau in the subalpine region of North Yatsugatake Mountains, the Middle Pleistocene volcano. The mother materials of soil consist of andesite, volcanic sand and ash. A_1 horizon is about 5 cm thick and elluviation is seen in some places. The water contents of soil (dry wt/wet wt $\times$ 100) in autumn were about 76% at 0—5 cm layer, 67% at 5—10 cm and 58% at 5—15 cm layer. The monthly mean temperatures are shown in Fig. 2. The annual rainfall is estimated at about 2,000 mm.

The area is covered with coniferous forest of *Abies veitchii*, *Tsuga diversifolia*, and *Picea hondoensis*, and *Betula ermani* is mixed with them. Growth of floor plants is thin, and moss cover is usual. The growing period of vegetation is from early June to late October, lasting for five months. The net-production of *Abies* forest of this region was estimated at about 11.1 ton d. w/ha/year and the amounts of annual litter supply captured by leaf traps were shown in Tab. II (K i m u r a 1963).

The decomposition rate of litter was estimated at 25% per year and the rate of accumulation (deposition-decomposition) at 3 mm/year in thickness. The annual decreasing rate of nitrogen in soil was estimated to be about 5% of total nitrogen amount. To discuss the rôle of community metabolism of soil animals in these situations is one of the aims of this work.

Surveys were made five times from early June to middle November of 1964. Each sample was taken from four (for macrofauna) or ten (for mesofauna) points settled at 30 m intervals along a linear line. The macrofauna was collected by hand sorting within a quadrat of 1/4 m² from three soil layers A_0, A_1 and A_2. The soil samples for extracting mesofauna were taken from four vertical layers each 5 cm deep. Small arthropods were extracted from 100 cc cores by modified Tullgren funnel, the cylinder of which were 6.5 cm in diameter. The soil was heated by a 40 W electric lamp for more than 24 hrs. *Enchytraeidae* were extracted from 200 cc cores by the 0. Nielsen method. *Nematoda* were extracted from 25 cc cores by Baermann funnels. The standing crops of mesofauna were calculated on the basis of the data given by other authors, leaving many problems which must be solved. Some values for respiration rates of macrofauna were obtained in our laboratory (N a k a m u r a 1965, S a i t o 1965). Otherwise the values given by others were adopted (M a c f a d y e n 1963). As for ingestion and defecation, the values given by E n g e l m a n (1961) for *Acari*, by N a k a m u r a (1965) for scarabaeid larva, by K ü h n e l t (1961) for *Diplopoda* and others were used. The defecation/ingestion ratio for *Nematoda*, *Neooligochaeta* and *Collembola* was tentatively assumed to be 0.5, a rather low value. By using these values monthly amounts of ingestion, defecation, assimilation, respiration and mortality of main animal groups were calculated. The amounts for one year were calculated as the total sum of these.

3. WORK IN THE COOL-TEMPERATE DECIDUOUS FOREST ECOSYSTEM

The working field of the cool-temperate deciduous forest was selected at Mt. Tanzawa (1500 m) and Mt. Gassan (1250 m), where natural forest of *Fagus crenata*, the representative cool-temperate deciduous tree species in Japan, is found. In these places, however, the study of seasonal changes in community metabolism of soil fauna was not made completely, and I will give here only the data obtained in the beech forest ecosystem of Mt. Tanzawa in May of 1963 for the comparison, citing the paper of Kitazawa, Saito and Nakamura (1964).

4. WORK IN THE WARM-TEMPERATE EVERGREEN BROAD LEAF FOREST ECOSYSTEM

A working field in warm-temperate evergreen broad leaf forest was selected at Mt. Kiyosumi, Chiba Prefecture. The basic rock is tertiary sandstone and the brown forest soil well developed. A_0 layer of soil is about 1 to 4 cm thick, A_1 layer about 5 to 10 cm and A_2 layer about 25—30 cm thick. The monthly mean soil temperatures of A_1 layer are shown in Fig. 2. Annual mean air temperature of the last 5 years is 14.0° C and mean annual rainfall is 2523 mm. The area is covered with such evergreen broad leaf trees as *Shiia sieboldi*, *Cyclobalanopsis stenophylla*, *Cleyera ochnacea*, *Camellia japonica* together with some large coniferous trees of *Abies firma* and *Cryptomeria japonica*. Floor plants are also evergreen. Plant production is continued throughout the year. The amount of litter supply in a year estimated by two methods: (i) the direct method using five leaf traps each 1 m^2 in size, (ii) the indirect method using allometric relation of diameter breast high to leaf amount. In the evergreen broad leaf forest of South Kyushu the relation

$$\log W = 1.89 \log D - 1.58,$$

was found, where W is dry weight of leaves in kg and D is DBH in cm (Kitazawa et al. 1959, Kimura 1960). By measuring DBH of every tree and applying above formula the amount of the leaves of Kiyosumi Forest which is considered to be equivalent to annual litter supply was estimated (Tab. III). The amounts estimated by the former method are less than those by the latter. The difference is considered to be caused, on the one hand, by translocation of leaf matter to the branches before the fall (Oland 1963), loss on leaching, grazing by animals and the corner effect of the square leaf trap, and on the other hand by using the formula $\log W = a \log D - b$ instead of $\log W = a \log D^2h + b$, being said to be more conformable, where h is the height of a tree (Ogawa, Yoda and Kira 1961). The measurements

of population numbers and standing crops of soil animals were made about monthly from May 1962 to Dec. 1963.

The relationship between the mean number per sample on a logarithmic plot, and the sample coefficient of variation of the main animal groups of this forest soil animal community is shown in Fig. 1. If the value of Student's t for the observed confidence limits, the coefficient of variation, C, and the ratio of the acceptable limit of the sampling error of the mean, E, are calculated, the required sample size, n, may be determined by the formula, $n \geqslant t^2C^2/\mathrm{E}^2$. Fig. 1 may be useful in determining the required size of quadrat for macrofauna and of soil core for mesofauna, which is related to the values of $\bar{x}$, C, t, E, and n.

5. THE ESTIMATED BIO-ECONOMIC VALUES

5.1 MONTHLY VALUES

Examples of monthly bio-economic values of main soil animal groups of the subalpine coniferous forest, the cool-temperate deciduous forest and the warm-temperate evergreen broad leaf forest ecosystem are shown in Tabs. IV, V and VI.

Monthly amounts of standing crops and respiration of macrofauna of the subalpine coniferous forest and warm-temperate broad leaf forest ecosystem are shown together with air temperature in Fig. 2, which represents the following trends.

Standing crops of macrofauna are less than those of mesofauna in the subalpine forest, while in the warm-temperate forest the relation is reverse.

Respiration of the macrofauna is less than that of the microfauna in both ecosystems, but this effect is especially marked in the subalpine forest ecosystem.

Standing crops of mesofauna of the subalpine forest ecosystem in summer season is not less than those of the warm-temperate forest ecosystem, while standing crops of macrofauna of the subalpine forest ecosystem is much less than those of the warm-temperate forest ecosystem.

In the warm-temperate region the seasonal changes in respiration, and its summer maximum, are clearly seen, but seasonal changes in standing crop are not pronounced.

5.2 ANNUAL VALUES

The amount of ingestion indicates the magnitude of activity of decomposition of litter and humus, defecation is related to the formation of the particulate

structure of soil, assimilation is equal to gross production and respiration is a measure of activity. Mortality includes predatory and non-predatory death, the latter of which is related to the liberation of nitrogenous compounds to the soil. The monthly values of these were summed up to give the annual values (Tab. VII).

The quantitative relations between litter supply, ingestion and respiration of primary consumers and respiration of macro-predators are diagrammatically shown in Fig. 3, which may show one aspect of the rôle played by the soil animal community in ecosystem metabolism. The respective values are larger in the warm-temperate ecosystem than in the subalpine ecosystem, reflecting the higher organic activity in the former. The ratio of decomposition by ingestion to the amount of litter supply is about 30% in the former and about 20% in the latter. This may suggest that in colder regions the accumulation of organic matter occurs more readily, related to the low rate of microbial litter decomposition, leading to subsequent carbonification and peat formation. In the alpine zone, this tendency is more marked, where the standing crop and litter supply of *Pinus pumila* community is fairly large, but the decomposition rate of litter is low, and the activity of soil fauna is very low.

6. CONCLUDING REMARKS

I have made this preliminary study so as to make a model of the rôle of the community metabolism of soil animals in ecosystem metabolism. The work was done under many assumptions and it involves many shortcomings. The methodological problems of such work may be emphasised by considering the shortcomings of this preliminary study. Serious shortcomings are involved in the studies of species composition, life history, generation and population structure, metabolism of the individual animal as a whole including ingestion, defecation, assimilation, respiration, mortality and growth, relation of metabolism to habitat factors, food habit and food chain, efficiency of extraction apparatus of mesofauna and estimation of numbers and standing crops (cf. Kitazawa 1959). The inter-species relations are almost neglected. The study of microfauna remains untouched. These deficiencies must be improved in the phase II of the IBP. It is of course desirable to carry out the study of secondary productivity in the same area as the study of primary productivity and of the ecology of soil microbes. To accomplish such synthesizing work, never easy, will be a task for the IBP.

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Table I

Three forest ecosystem types in Japan

Altitudinal zone	Climatic zone	Vegetation type	Main tree species	Station
Subalpine 1700—2500 m	sub-arctic 6—0°C (annual mean)	evergreen coniferous forest	*Abies veitchii* *Tsuga diversifolia* *Betula ermani*	North Yatsugatake Mts. 2150 m
Montane 700—1700 m	cool-temperate 12—6°C	deciduous forest	*Fagus crenata* *Quercus crispula*	Mt. Tanzawa 1500 m
Basal 0—700 m	warm-temperate 18—12°C	evergreen broad leaf forest	*Shiia sieboldi* *Cyclobalanopsis stenophylla* *Camellia japonica*	Mt. Kiyosumi 300 m

Table II

Amounts of litter supply in the subalpine coniferous forest of North Yatsugatake Mountains, calculated from Kimura's data

Litter	g d.w./m^2/year	Kcal/m^2/year
Needles	220	1210
Deciduous leaves	30	144
Branches, barks, cones, seeds	170	799
Total litter supply	420	2153

Table III

Amounts of litter supply per m^2 in the warm-temperate evergreen broad leaf forest of Mt. Kiyosumi

Values estimated by leaf traps			Values estimated from DBH		
	Dry weight (g)	Cal		Dry weight (g)	Cal
Broad leaves	481	2,309	Tree leaves	1,327	6,400
Needles	207	1,141	Floor plants	34	163
Twigs	157	740	Total litter supply	1,361	6,563
Seeds, feces	80	383			
Floor plants	34	163			
Total litter supply	959	4,736			

Table IV

An example of the data on community metabolism of soil animals of the subalpine coniferous forest ecosystem in July 1964 of North Yatsugatake Mountains

Animal groups		Numbers/m²	Wet weight	Resp. rate cal/g/day at 13°C	Resp.	Assimil.	Ingest.	Defecat
							Kcal/m²/month	
Oligochaeta		27	0.8	6	0.1	0.2	0.4	0.2
Diplopoda		36	0.1	10	0.0	0.0	0.1	0.1
	Scarabaeidae	33						
Coleoptera larvae	*Elateridae*	9	2.2	16	1.1	1.4	6.9	5.5
	Curculionidae	2						
Diptera larvae		29	0.1	24	0.1	0.1	0.2	0.1
Orthoptera		5	0.2	58	0.3	0.5	1.7	1.2
Collembola		61	0.1	117	0.4	0.4	0.8	0.4
Total macrodecomposers		(217)	3.8		2.1	2.9	10.8	7.9
Nematoda		1.8×10^5	0.2	117	0.7	0.9	1.8	0.9
Enchytraeidae		0.9×10^4	1.0	81	0.2	0.6	1.1	0.5
Acari		0.2×10^5	0.2	58	0.3	0.4	1.5	1.1
Collembola		0.64×10^5	6.4	117	22.5	24.7	49.4	24.7
Diptera larvae		750	3.8	24	2.7	3.6	7.1	3.6
Total mesodecomposers			11.6		26.5	30.2	61.0	30.8
Hirudinea		2	0.2	12	0.1			
	Scolopendromorpha	4						
Chilopoda	*Lithobiomorpha*	13	0.3	87	0.8			
	Geophilomorpha	7						
Symphyla		7						
Araneina		34	0.1	22	0.1			
Carabidae imagines		4	0.2	32	0.2			
Carabidae larvae		8	0.1	16	0.1			
Staphylinidae imagines		3	0.1	32	0.1			
Staphylinidae larvae		8	0.0	16				
Total macropredators		91	1.0		1.4			

Table V

An example of the data on community metabolism of soil animals of the cool-temperate deciduous forest ecosystem in May, 1963 at Mt. Tanzawa (Kitazawa, Saito and Nakamura 1964)

Animal groups	Numbers / m^2	Wet weight g/m^2	Resp. rate at 8.6°C cal/g/day	Resp. $Kcal/m^2$ month
Oligochaeta	47	6.2	3.3	0.6
Gastropoda	24	0.3	5.7	0.05
Crustacea	23	0.2	17	0.1
Diplopoda	11	0.1	8	0.02
Coleoptera larvae	19	0.6	12	0.2
Total macrodecomposers	124	7.4		1.0
Nematoda	1.25×10^5	0.2	90	0.6
Enchytraeidae	0.49×10^4	0.8	39	0.9
Oribatidae	0.90×10^5	0.1	7.7	0.02
Collembola	0.78×10^5	13.0	71	28.0
Diptera larvae	3,419	1.5	18	0.8
Total mesodecomposers		15.6		30.3
Hirudinea	3	0.3	(10)	(0.9)
Chilopoda	83	0.7	67	1.4
Araneina	90	0.37	39	0.4
Coleoptera imagines	17	0.6	18	0.3
Total macropredators	193	1.97		3.0

Table VI

Data on community metabolism of soil animals of the warm-temperate evergreen broad leaf forest ecosystem in July 1963 at Mt. Kiyosumi

Animal groups		Numbers/m^2		Wet weight g/m^2	Resp. rate cal/g/day at 22°C	Resp.	Assimil.	Ingest.	Defecat.
						Kcal/m^2/month			
Oligochaeta		57		13.0	11	4.4	6.6	13.2	6.6
Gastropoda		45		0.4	18	0.2	0.2	0.4	0.2
	Ligidium	190							
Crustacea	*Armadillidium*	82	311	5.4	55	9.2	11.0	44.0	33.0
	Porcellio	11							
	Orchestia	28							
	Glomeromorpha	1							
Diplopoda	*Polydesmoidea*	29	61	2.1	20	1.3	1.7	6.8	5.1
	Juliformia	31							
Hemiptera	*Cicadidae*	4		0.2	29	0.2	0.2	1.0	0.8
Coleoptera larvae	*Scarabaeidae*	2	7	1.8	29	1.6	2.1	10.5	8.4
	Elateridae	5							

Total macrodecomposers		501		22,9		16.9	21.8	75.9	54.1
Nematoda		1.68×10^5		0.2	220	1.4	1.8	3.6	1.8
Enchytraeidae		1.33×10^4		1.5	150	7.0	17.4	31.3	13.9
Acari		0.58×10^5		0.6	110	2.0	2.3	9.2	6.9
Collembola		0.59×10^5		5.9	220	40.2	44.3	88.6	44.3
Diptera larvae		1,294		6.5	44	8.9	11.5	23.0	11.5
Total mesodecomposers		3.00×10^5		14.7		59.5	77.3	155.7	78.4
Turbellaria		1							
Hirudinea		3	4	1.1	29	1,0			
	Scolopendromorpha	2							
Chilopoda	*Lithobiomorpha*	6	30	0.9	160	6.5			
	Geophilomorpha	21							
	Symphyla	1							
	Acarina	16	82	0.6	41	0.8			
Arachnida			82	0.6					
	Araneina	66							
	Carabidae imagines	2			59	0.2			
Coleoptera			3	0.1		6.5			
	Carabidae larvae	1							
Total macropredators		120		2.7					

Table VII

Total metabolism of soil animal community of the subalpine coniferous forest and warm-temperate evergreen broad leaf forest ecosystem. $Kcal/m^2$

Ecosystem type	Soil fauna	Ingest.	Defecat.	Assimilation	Resp.	Mortality
Subalpine Coniferous forest	macrofauna mesofauna	39 368	28 184	11 184	8 150	3 34
	total	407	212	195	158	37
Warm-temperate evergreen broad leaf forest	macrofauna mesofauna	595 951	431 485	164 466	123 355	41 111
	total	1,545	916	629	479	150

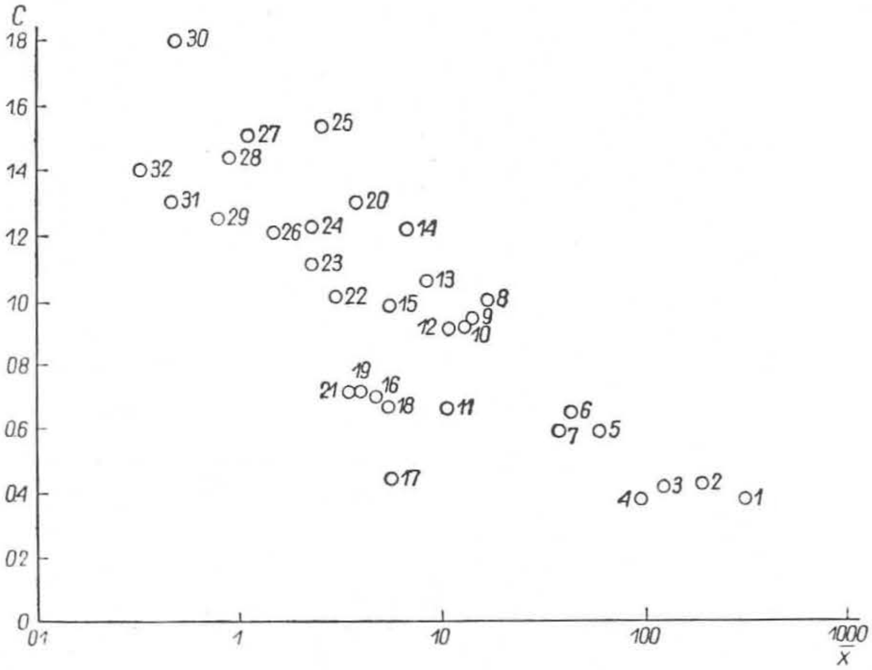

Fig. 1. Relations of mean number per sample $\bar{x}$, and coefficient of variations C of main soil animal groups of the warm-temperate broad leaf forest ecosystem at Mt. Kiyosumi in Dec. 1963

The sample size $n = 24$, volume of core is 25 cc for *Nematoda*, 100 cc for *Acari* and *Collembola*, 200 cc for *Enchytraeidae*. A quadrat for macrofauna is 25×25 cm^2 in area

1 — meso-*Arthropoda*, *2* — *Acari*, *3* — *Collembola*, *4* — *Nematoda*, *5* — total macrofauna, *6* — total macrodecomposers. *7* — macrofauna (0—5 cm deep), *8* — macrofauna (5—30 cm deep), *9* — *Crustacea*, *10* — *Isopoda*, *11* — macropredators, *12* — *Diplopoda*, *13* — *Ligidium*, *14* — *Polydesmoidea*, *15* — macro-*Collembola*, *16* — *Arachnoidea*, *17* — *Enchytraeidae*, *18* — *Neooligochaeta*, *19* — *Chilopoda*, *20* — *Juliformia*, *21* — *Araneina*, *22* — *Armadillidium*, *23* — *Geophilomorpha*, *24* — *Porcellio*, *25* — *Gastropoda*, *26* — macro-*Acarina*, *27* — macro-*Nematoda*, *28* — *Orchestia*, *29* — *Lithobiomorpha*, *30* — *Scolopendromorpha*, *31* — *Coleoptera* larvae, *32* — *Cicadidae* larvae

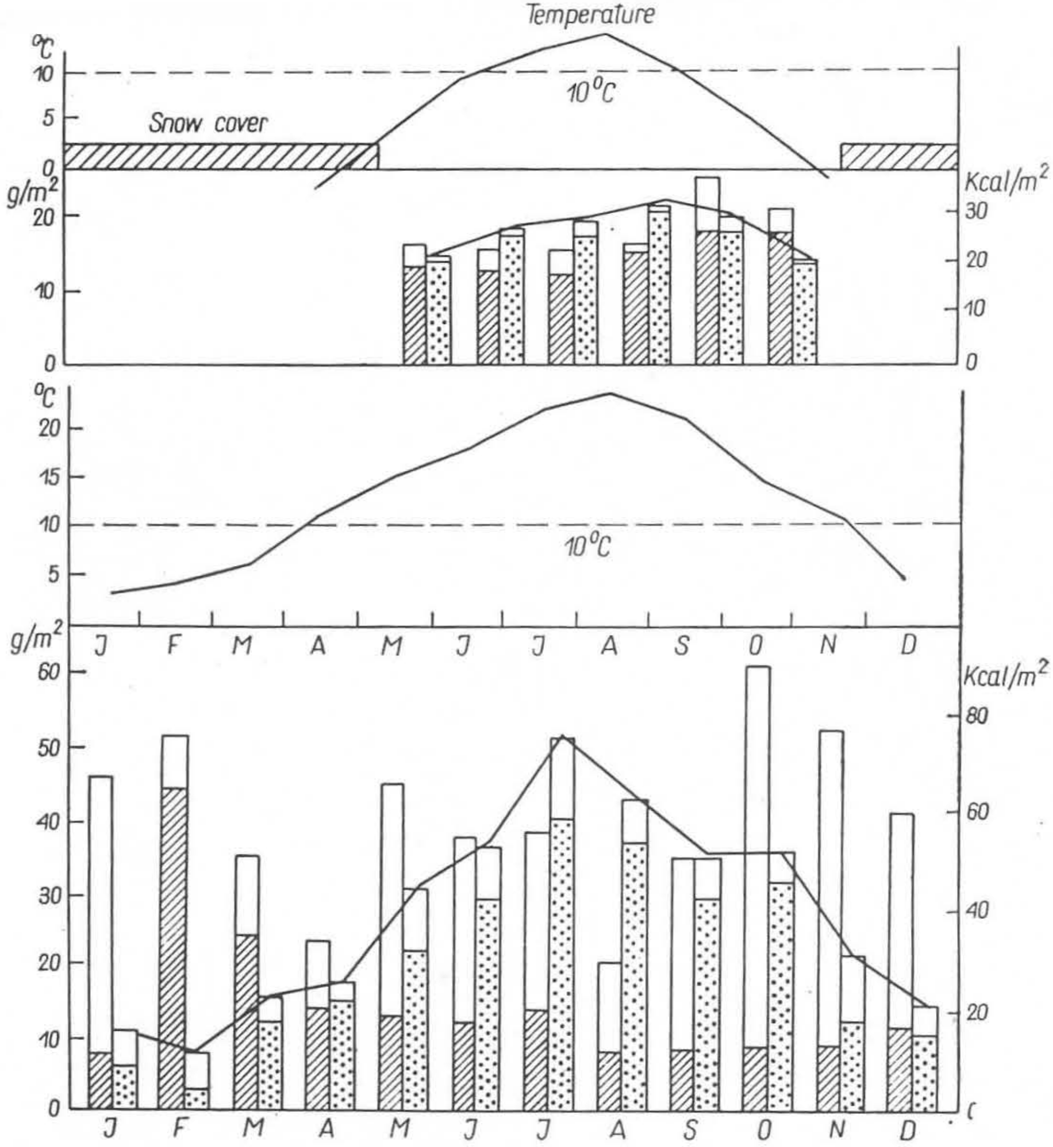

Fig. 2. Seasonal changes in standing crops (left column) and respiration (right column) of macrofauna (blank part) and mesofauna (hatched and dotted part) of the subalpine coniferous forest ecosystem (above) and the warm-temperate broad leaf forest ecosystem (below) of central Japan

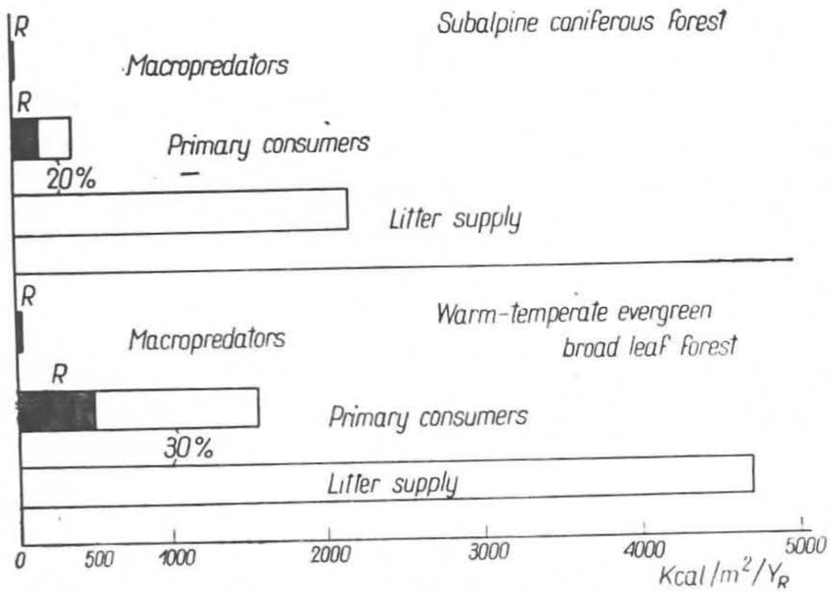

Fig. 3. The relations between the amounts of litter supply, ingestion or decomposition of litter or humus by primary consumers, the respiration of primary consumers and macropredators